

A REVIEW OF *HETEROPORODRILUS* FROM SOUTH-EAST QUEENSLAND
(ANNELIDA: OLIGOCHAETA)

ROB J. BLAKEMORE

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The endemic earthworm *Heteropodrilus* Jamieson, 1970, is revised to accommodate four new species, plus new combinations mainly from *Plutellus* s. lat., that raise the generic total from ten to nineteen species. Previous emendments to these two genera, both of which display nephropore alternation, had reduced primary differentiation to absence or presence of stalks on the calciferous glands. In the current revision, however, the form of prostatic glands is considered more definitive. Possession of tubular prostates qualifies *Plutellus*, now restricted to three known species, while in *Heteropodrilus* there is development from this plesiomorphic state to the more derived racemose or tubuloracemose form of prostate. *Heteropodrilus* has an extensive distribution in the eastern subregion of Australia yet it appears especially diverse in south-east Queensland, compared to *Plutellus* s. strict. that is mainly restricted to central coastal New South Wales. Redescription of the type species of both genera, *H. tryoni* and *P. heteroporus*, confirms the basis of this revision. The distributions and ecology of these and other described species are considered and new keys to genera are provided. □ *Heteropodrilus*, *Plutellus*, calciferous glands, taxonomy, earthworm ecology.

R.J. Blakemore, University of Queensland, St Lucia, Queensland 4072, Australia; current address; c/o CSIRO Division of Entomology, PO Box 1700, Canberra, Australian Capital Territory 2601, Australia; 15 March 1993.

The current study resulted from part of a project investigating the distribution and ecology of earthworms in managed soils and their effects on soil fertility in south-east Queensland. Surveys located 44 exotic species that were often abundant and widely distributed, as well as 41 native taxa that were generally more restricted in their distributions. This paper concerns the indigenous *Heteropodrilus* Jamieson, 1970 that has not been extensively revised since its designation. This genus is frequently encountered in the wider Brisbane region.

Fletcher (1889) was the first to recognise a well-marked group of species (which he nevertheless referred to *Cryptodrilus*, Fletcher, 1886) sharing, amongst other characters, nephropore alternation. It was left to Jamieson (1970) to formally define *Heteropodrilus* for ten (plus one dubious) 'heteropore' species, many of which were by then assignable to *Woodwardiella* Stephenson, 1925. In the same paper, a restriction of the heterogeneous assemblage attributed to *Plutellus* Perrier, 1873 was suggested (as envisaged by Gates, 1961), as only *P. manifestus* (Fletcher, 1889) from central New South Wales appeared to be congeneric with *P. heteroporus*, the type-species. Re-description of type material confirmed the basis for a restriction of *Plutellus*

to species with tubular prostates, but this was deferred (Jamieson, 1971a,b). A numerical analysis by Wallace (1972) confirmed these groupings even though prostate morphology was withheld as an attribute.

In order to accommodate two new heteropore species from Queensland that bore racemose prostates it was necessary for Jamieson & Nash (1976) to emend the generic definition of *Plutellus* to include both tubular and racemose prostates thus reducing the distinction from *Heteropodrilus*. Such 'infrageneric variation' was used by these latter authors to 'strongly refute' the use of racemose prostates to distinguish a family Megascolecidae from a family Acanthodrilidae with tubular prostates (and holonephridia) as advocated by Gates (1959) and rejected by Jamieson (1971). However, a primitive 'plutelloid' from Lord Howe Island (Jamieson, 1977) seemed to have more in common with its congeners in New South Wales. The definition of *Plutellus* was further modified by Dyne (1981) to receive three new species from the periphery of the Morton Bay Region, bringing the generic total to eight, and the 'tenuous' distinction from *Heteropodrilus* was reduced principally to the presence or absence of stalks to the calciferous glands.

The wide distribution of *Heteroporodrilus* from Queensland to Victoria corresponds in part with various riverine systems (Jamieson, 1970). It appears especially aggregated, or rather the reports are more frequent, in the Brisbane region of south-east Queensland. In contrast, *Plutellus* s. lat., was recorded further south in coastal New South Wales and just to the south and north of Brisbane. Dyne (1981, 1984) found this distribution pattern enigmatic because no appreciable biogeographic barriers intervened. He also intimated that should intermediate forms with short-stalked calciferous glands be found, it would be doubtful that the two genera could remain discrete.

The present study contends that just such intermediate forms already existed in *Plutellus* s. lat., moreover 'short-stalked' calciferous glands had also been confirmed in *Heteroporodrilus*, but the consequences are here interpreted in a different manner. The apparent discontinuity of the distributions is largely resolved by revision of the definitions of both genera, based on new material and re-examination of previous accounts, resulting in an amalgamation of the 'northern' heteropores while maintaining the 'central' plutelloids as a discrete zoogeographic and phyletic entity.

CONVENTIONS

Original illustrations, drawn using a Wild M5 microscope with camera lucida, have shaded clitella. All scale bars represent 1mm.

Abbreviations used are: i ii etc., segments numbered from the peristomium; ii/ iii/ etc., on ii, on iii etc.; 1/2 2/3 etc., intersegmental furrows, i.e., between i and ii etc.; a b etc., individual setae from the ventralmost on each side; A B etc., longitudinal series between setae a setae b etc.; g.m. genital marking; n.p. nephropore; NSW, New South Wales; Qld., Queensland, QMG, Queensland Museum registration number; sp.p., spermathecal pore; ; U. (convention from German) circumference. Setal ratios, of debatable systematic importance, follow the formula (xii/aa:ab:cd:dd:μ).

SYSTEMATICS

Heteroporodrilus is emended to accommodate the new species, and to receive several species that were previously placed in *Plutellus* (sensu Jamieson & Nash, 1976; Dyne, 1981). The revision proceeds in three stages. First, at least two species (*H. jamiesoni* sp. nov. and *H. ox-*

leyensis) belonging to the established *Heteroporodrilus*, are found to have short-stalked calciferous glands thereby expanding the generic definition to species with sessile or short-stalked calciferous glands. Hence the distinction from *Heteroporodrilus* of the only '*Plutellus*' species reported from Queensland, *P. incommodus*, *P. raveni* and *P. notatus*, which are all described with similar short-stalks, is removed. Secondly, expanding the definition to include Dyne's (1981) 'intermediate' species with short-stalked glands and racemose or tubuloracemose prostates absorbs the two species from northern New South Wales, *P. minyoni* and *P. clarkei*. Thirdly, *Plutellus* is restricted to only those species with tubular prostates and long-stalked calciferous glands.

This division is especially strong as no genetic correlation between prostate form and calciferous nexus is implied. Tubular prostates are generally considered the plesiomorphic condition, thus *Heteroporodrilus* can be viewed as a derived, apomorphic sibling group of a more primitive *Plutellus*. The above split has the added convenience of making the geographic distributions disjunct with *Plutellus* confined to the coastal region of central New South Wales (two species) and Lord Howe Island (one species) and the remainder in *Heteroporodrilus*, chiefly in south-east Queensland and northern New South Wales. The question of the phyletic relationships of the Lord Howe Island plutelloids, is not ventured here.

Heteroporodrilus

Jamieson, 1970 emend.

TYPE SPECIES

Heteroporodrilus tryoni (Fletcher, 1890) from Milton, Brisbane.

DIAGNOSIS

Moderate to large size terrestrial worms (52-580mm long) generally with less than 200 segments (range 90-387). Sometimes dorsum canaliculate and with or without brown-grey pigmentation. Prostomium variable from propilobous to tanylobous, often grooved. Setae 8 per segment (only occasionally a and/or b retained on xviii). Dorsal pore from 5/6 or beyond. Male pores and pores of one pair of racemose to tubuloracemose prostates in xviii. Spermathecal pores 2-5 pairs, the last in 8/9 (*H. notatus* and *H. clarkei* near mid-ix). Nephropores conspicuous at the anterior border of their segments in D lines in ii-iv or v; in C lines, or

alternating between D and C (or mid-BC) for a few segments; then from x where alternation between B and D lines commences for the remainder of the body (may be asymmetrical).

Gizzard in v. Calciferous glands, 3-5 ventrolateral pairs sessile or on short-stalks (i.e. about as long as broad) on the oesophagus, the last pair always in xiii. Spermathecae have one or more, discrete or composite, diverticula. Holonephric with (adiverticulate but sometimes bilobed) terminal bladders. Holandric, testis and funnels free or in unpaired (pericardiac) testis sacs.

DISTRIBUTION

Murray-Darling River basins in NSW and South Australia; the Wimmera River, Victoria; Tweed River basin in northern NSW; river-catchments in south-east Qld.

SPECIES OF HETEROPORODRILUS

The numbers and conditions of specimens inspected in previous definitions (in brackets) indicates the stability of those descriptions. Only species with an asterisk are (re)described in this paper.

1. **H. bongeen* sp. nov. from Bongeen, Qld.
2. *H. canaliculatus* (Fletcher, 1889) from Lachlan River, Forbes, NSW.
Cryptodrilus canaliculatus Fletcher, 1889: 1534-1536 (twelve specimens, poorly preserved); Fletcher, 1890: 996.
Plutellus canaliculatus; Michaelsen, 1900.
Heteroporodrilus canaliculatus; Jamieson, 1970: 111-112 (types no longer traceable).
3. *H. clarkei* (Dyne, 1981) comb. nov. from Whian Whian State Forest, northern NSW.
Plutellus clarkei Dyne, 1981: 97, figs 1a; 2c, e; table 1 (three specimens)
4. *H. cooraniensis* (Spencer, 1900) from Cooran, Qld.
Cryptodrilus cooraniensis Spencer, 1900: 42-43, figs 34, 35, 36 (spirit specimens); Sweet, 1900: 114; Jensz & Smith, 1969: 86 (only one questionable syntype remains in reasonable condition).
Woodwardia cooraniensis; Michaelsen, 1907: 162; Bage, 1910: 234-236, figs 18-21.
Heteroporodrilus cooraniensis; Jamieson, 1970: 112-113 (material not available).
5. **H. dioecius* (Stephenson, 1933) from Toowoomba, Petrie, Brookfield and Samford (new record), all in Qld.
Woodwardiella dioecia Stephenson, 1933: 910-912, figs 9; 10 (four clitellate specimens).

Heteroporodrilus dioecius; Jamieson, 1970: 113-114, figs 5d-f; 9b; 10b, c (four clitellate and one a clitellate specimens).

6. **H. doubei* sp. nov. from Lismore, NSW.
7. *H. incommodus* (Jamieson & Nash, 1976) comb. nov. from Eudlo Creek and Forest Glen, Qld.
Plutellus incommodus Jamieson & Nash, 1976: 47-49, figs 1: a, b; 2a-g; table 1 (14 specimens).
8. **H. jamiesoni* sp. nov. from Mt Glorious, Qld.
Heteroporodrilus ashworthi (Stephenson, 1933) syn. nov. (part, Mt Glorious specimen non Stephenson, 1933 specimen) sensu Jamieson, 1970: 109-111, figs 2; 3a; 8a,b; 9a; 10a (one clitellate specimen).
Note: *H. ashworthi* sensu Jamieson (1970) is not the same as *W. ashworthi* Stephenson, 1933, but represents a new species. Since *W. ashworthi* is a junior synonym of *H. oxleyensis* (Fletcher, 1889) the name *ashworthi* is unavailable and *H. ashworthi* sensu Jamieson (1970) is described herein as *H. jamiesoni* sp. nov.
9. *H. lamingtonensis* (Jamieson, 1970) comb. nov. from O'Reilly's, Lamington Nat. Park, Qld.
Plutellus lamingtonensis Jamieson, 1970: 115-117, figs 5a; 9c; 10d (a single specimen).
10. *H. mediterreus* (Fletcher, 1887b) from banks of the Darling River between Bourke and Brewarrina NSW; Gragin and Warialda, NSW.
Cryptodrilus mediterreus Fletcher, 1887b: 614-616 (ten specimens - lost).
Heteroporodrilus mediterreus Jamieson, 1970: 117-120, figs 4a,b,e,f,g; 9d; 10e (six poor specimens, only two clitellate).
Note: The records by Jamieson (1970: 119) for this species in Victoria are incorrect.
11. *H. minyoni* (Dyne, 1981) comb. nov. from Whian Whian State Forest, northern NSW.
Plutellus minyoni Dyne, 1981: 100-102, figs 1b; 2a, b, d; table 1 (a single intact specimen and several anterior amputees).
12. *H. notatus* (Dyne, 1981) comb. nov. from Cooroy, Qld.
Plutellus notatus Dyne, 1981: 102-104, fig 3 a-e; table 1 (three specimens).
13. **H. oxleyensis* (Fletcher, 1889) from Oxley; Brookfield (new record), Samford (new record) and Mt Cotton (new record), all near Brisbane, Qld.; ?Marrickville, NSW.
Cryptodrilus Oxleyensis Fletcher, 1889: 1537-1538. (one complete but a clitellate specimen and two other "more or less incomplete specimens").

- Plutellus fletcheri* (part); Michaelsen, 1900: 173 (excluding *Cryptodrilus fletcheri* Beddard, 1887).
Woodwardia oxleyensis; Michaelsen, 1907: 162.
Heteropodrilus oxleyensis Jamieson, 1970: 120-122, figs 3b-e; 5g; 9e; 10f,g (two clitellate specimens).
Woodwardiella ashworthi Stephenson, 1933: 912-914, figs 11-13, syn. nov. (a single clitellate specimen).
Heteropodrilus ashworthi; Jamieson, 1970: 109-111 (part excluding Mt Glorious specimen).
14. *H. raveni* (Jamieson and Nash, 1976) comb. nov. from Forest Glen, Qld.
Plutellus raveni Jamieson & Nash, 1976: 50-52, figs 2h-j; 3, table 1 (six specimens).
15. *H. shephardi shephardi* (Spencer, 1900) from Horsham, (and Dimboola?) Victoria (Wimmera River).
Cryptodrilus shephardi Spencer, 1900: 40-41, figs 28, 29, 30, ("spirit specimens"); Jenz & Smith, 1969: 91 (three lectotypes remain).
Woodwardia shephardi; Michaelsen, 1907: 162.
Heteropodrilus shephardi shephardi Jamieson, 1970: 122-124, figs 4c,d; 9f; 10i (a paralectotype specimen).
16. *H. shephardi armatus* Jamieson, 1974 from Penola and Naracoorte, Victoria (about half a dozen specimens).
Heteropodrilus shephardi armatus Jamieson, 1974: 85-87, figs 2b; 10b; 11a; 13, table 3 (four or five specimens).
17. *H. sloanei* (Fletcher, 1889) from Coonabarabran, NSW.
Cryptodrilus Sloanei Fletcher, 1889: 1536-1537, (four acitellate specimens and one doubtful juvenile).
Plutellus sloanei; Michaelsen, 1900.
Heteropodrilus sloanei; Jamieson, 1970: 124, (three desiccated specimens).
 Note: Jamieson (1970) considered synonymy with *H. canaliculatus* and *H. lamingtonensis* dependent on availability of new material.
18. **H. thompsoni* sp. nov. from Brookfield, Qld.
19. **H. tryoni* (Fletcher, 1890) from Milton, Sherwood, Brookfield and Toowong suburbs of Brisbane; Binna Burra, Lamington National Park; Mt Glorious; Mt Mee and Nambour, all in Qld.
Cryptodrilus Tryoni Fletcher, 1890: 994-996, (one poorly preserved specimen).
Plutellus tryoni; Michaelsen, 1900: 171.
Woodwardia (?) tryoni; Michaelsen, 1916: 62.
Woodwardiella tryoni; Boardman, 1932: 127-128 (a single, poorly preserved specimen).
- Heteropodrilus tryoni*; Jamieson, 1970: 125-129, figs 5b,c; 8c,d; 9g,h; 10j (nine clitellate specimens).
Woodwardiella youngi Boardman, 1932: 128-130, fig 2 (two specimens).

SPECIES INCERTAE SEDIS

- ?*Heteropodrilus fletcheri* (Beddard, 1887), provenance in Qld. unknown.
Cryptodrilus fletcheri Beddard, 1887: 544-548, illustr. (two specimens, one mature - types lost).
Plutellus fletcheri; (part excluding *H. oxleyensis*) Michaelsen, 1900: 79.
Heteropodrilus ? fletcheri; Jamieson, 1970: 114-115.
 Note: Based on inadequacies of the original account, Jamieson (1970) considered this species to be 'nomen et species dubium' but its affinity with *H. oxleyensis* was alluded to by Michaelsen, 1900.
 A large heteropore specimen, unfortunately too macerated for adequate characterisation, was collected by C.H. Thompson in 1984 from Mt Buderim near Maroochydore, Qld. It had the external appearance of *H. shephardi* and three pairs of spermathecae. Two unpublished new species from south-east Qld. have been identified by Dyne (1984) and a further two species from the Adelaide region are currently in preparation by the author.

KEY TO HETEROPODRILUS

1. Large size (250mm); five pairs of calciferous glands; three pairs of spermathecae . . . *H. tryoni*
 Four pairs of calciferous glands 2
 Three pairs of calciferous glands 10
2. Three pairs of spermathecae 3
 Two pairs of spermathecae 8
3. Nephropores alternate between *c* line and *d* line in 4/5-8/9 (from Queensland) 4
 Nephropores alternate between *d* line and mid-*bc* in 4/5-8/9 (Victoria and South Australia) . . . 7
4. Prostates confined to xviii, penial setae absent; genital markings usually in xx 5
 Prostates xvii-xix or xvi-xxii, penial setae present; no genital markings in xx 6
5. Prostates with straight duct; spermathecal diverticula variable, single or paired . . . *H. incommodus*
 Prostates ducts long and sinuous; spermathecae each with a single, simple diverticulum . . . *H. raveni*
6. Dorsum canaliculate; spermathecae each with two diverticula, occasionally single, but often compound; seminal vesicles in ix and xii *H. canaliculatus*
 Body circular; spermathecae each with a single, simple (even rudimentary) diverticulum; seminal vesicles in xi and xii *H. mediterraneus*

7. Genital markings as eye-like pits in 17/18 and 18/19; penial setae present in xviii
 *H. shephardi armatus*
 Genital markings segmental in some or all of xvii, xviii and xix; penial setae absent
 *H. shephardi shephardi*
8. Spermathecal diverticula bifid or trifid or variously multi-lobed or numerous, genital markings in x (or xi) 9
 Spermathecae with simple (paired) diverticula
 *H. bongeen* sp. nov.
9. Size 210mm; prostomium epilobous furrowed; spermathecae with large and concertinaed ampullae and compound diverticula
 *H. thompsoni* sp. nov.
 Size <105mm; prostomium tanylobous; spermathecae, with simple or bifid diverticula, opening to midsegment *H. notatus*
10. Spermathecae, three or more pairs 11
 Spermathecae, two pairs 14
11. Size generally 100mm; genital markings in xvii-xx 12
 Size generally <100mm; genital markings weak or absent (immature?) 13
12. Spermathecae 5 (or 4) pairs; genital markings widely paired in xvii-xx, presetal in xvii
 *H. jamiesoni* sp. nov.
 Spermathecae 4 (or 3) pairs; postsetal genital markings elongate or closely paired in xvii-xx
 *H. oxleyensis*
13. Spermathecae 3 pairs each with two diverticula
 *H. sloanei*
 Spermathecae 3 pairs (occasionally one of the six absent) each with a single diverticulum; prostates absent or present *H. dinecius*
14. Spermathecal pores segmental, presetal in xviii and ix *H. clarkei*
 Spermathecal pores intersegmental in 7/8 and 8/9 15
15. Size 300; prostomium epilobous; preclitellar genital marking a series of papillae within tumid ventral pads in xii, xvii-xxi *H. minyoni*
 Size 100; prostomium epilobous; preclitellar genital markings in vii, viii and ix; spermathecal diverticula paired *H. doubei* sp. nov.
 Size <80; prostomium tanylobous; preclitellar genital markings widely paired or lacking 16
16. Spermathecal diverticula paired *H. lamingtonensis*
 Spermathecal diverticula single *H. cooraniensis*

Associations between species can be inferred from their nearness in the above key. Accounts of species not covered in the following descriptions may be sought with reference to the preceding species list.

DESCRIPTIONS OF SPECIES

Heteroporodrilus bongeen sp. nov. (Fig. 1)

MATERIAL EXAMINED

HOLOTYPE: QMG210136, opposite the local school house at Bongeen (27°34'S; 151°27'E) on the Condamine River plain west of Toowoomba, Qld, R.J. Blakemore, 09 Apr 92, drawn and dissected, posterior amputee.

PARATYPE: same collection data as holotype. QMG210137, dissected, posterior amputee.

OTHER MATERIAL: same collection data as holotype. QMG210138, two anterior amputees (losing first 5-7 segments); also collected were four damaged sub adults.

HABITAT

Under bare soil in dark brown cracking clays, Waco clay gilgai complex (Beckmann & Thompson, 1960) on roadside next to cultivated fields.

EXTERNAL CHARACTERS

Length 250+mm, body circular in section without dorsal groove although one specimen had the posterior 6 segments furrowed. Width 5.5-7.5mm, widest point about viii.

Mass 3-4g per adult. Segments 193-200, first ten segments smooth followed by moderate secondary annulation in succeeding segments. Colour dark slate grey pigmented anterior (with paler ventral tumescences on x, xi and possibly xii), dorsum and caudal segments with faint red/yellow iridescence; mid-body moderate pigmentation (soil visible in gut). Clitellum variously darker or lighter brown colour. Prostomium open epilobous or closed by fine groove but appearing tanylobous due to longitudinal dorsal groove extensions which may almost reach as far as 1/2. First dorsal pore 10/11? (difficult to determine due to deep furrows). Setae small, 8 per segment from ii, *a* and *b* obscure (modified?) on xviii, lateral setal couples *cd* widely spaced (mean of two ratios, 1.7:1.0:1.4:2:4:0.28). Nephropores in D line 1/2-3/4, 6/7, 8/9, 10/11 or 11/12 then alternating; in B line 5/6, 11/12 or 12/13 then alternating, possibly in C line in 4/5-7/8. There is slight variation between specimens, but for most of the body length there is clear alternation between B and D lines. Clitellum 1/3xiii-xvii annular, setae and nephropores retained. Male pores minute in xviii on small raised porophores in B line. Female pores paired in xiv in line of anterior annulus within a common

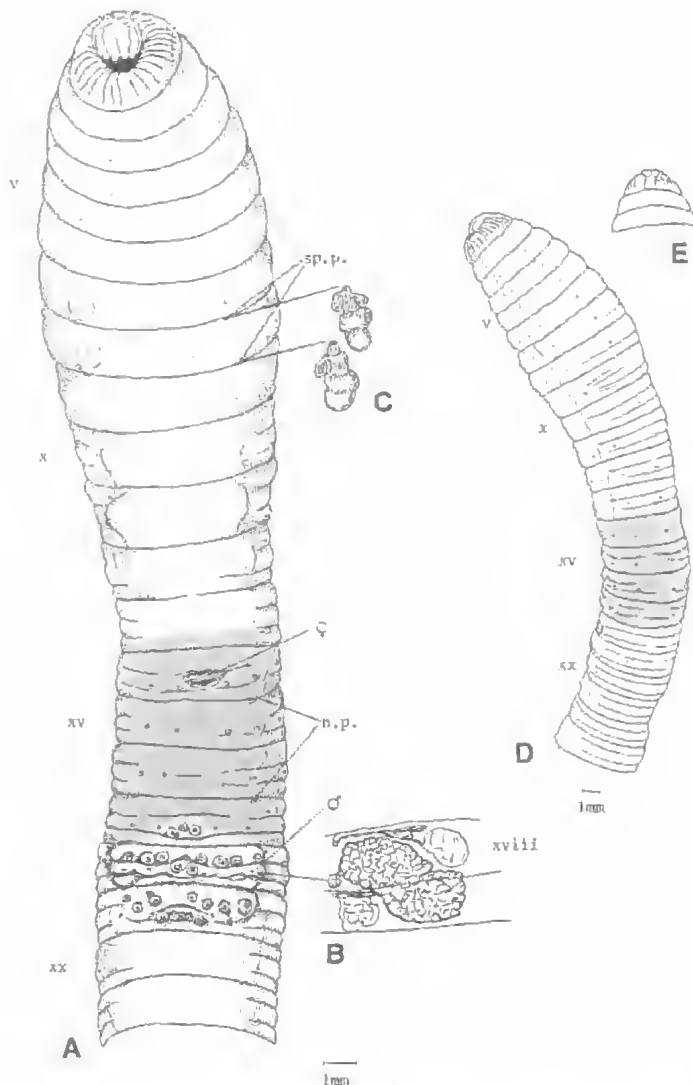


FIG. 1. *Heteroporodrilus bongeen* sp. nov. A, ventral view of H specimen; B, prostate (with two adjacent nephridia); C, spermathecae in situ; D, reduced lateral view; E, prostomium.

darker patch antero-medial to *a* setae. Spermathecal pores 7/8 and 8/9 in B line concealed in deep intersegmental furrows. Genital markings (x-xii ventrally tumid?), in xvii almost central between *a* setae, three small discs in raised tumid area; in xviii, especially in anterior annulus, four or five pairs of discs (one pair ventral in setal arc) in furrowed, generally tumid area that fills the ventral aspect; in xix similar markings, but discs tend to be smaller and more numerous.

INTERNAL CHARACTERS

Septa 4/5-11/12 getting progressively thicker, from 12/13 becoming weaker (10/11-12/13 thickest); pharyngeal ligatures (tendons) extend beyond viii. Dorsal blood vessel single, continues on pharynx. Commissurals in vi-ix, larger hearts in x-xiii. Gizzard compact, spherical and muscular in v. Calciferous glands four pairs, compact and ventral on oesophagus in x, xi, xii, and xiii; those in x smaller, almost rudimentary. Oesophagus narrows in xiv (valve?) then widens in xv as intestine proper; typhlosole not found. Holonephridia, a pair in each segment, from at least v, with large deflated and flattened, spherical terminal bladders. Nephridia closely associated with anterior septa (pre-septal funnels). Male organs holandric: iridescent funnels of testes in x and xi; racemose seminal vesicles in ix and xii. Ovaries in xiii, ventrally paired sheets of mesentery may be ovaries but individual oocytes not seen, the egg funnels were seen on the posterior septum. Five or six smallish, white spheres were noted in one specimen loosely attached to the septum, possibly parasitic *Monocystis* sp? Prostates a pair of large tongue-like racemose glands extending from xviii-xix and overlying a small, flaccid duct that soon enters the body wall. Spermathecae two pairs in viii and ix: waisted ampullae clearly demarcated from shorter ducts, each bearing a pair of opposed digitiform, iridescent diverticula.

One specimen had a single diverticulum on only one of its spermathecae. Gut contents fine grey clay soil and a few round grits coated in mucus (i.e. geophagous).

TAXONOMIC REMARKS

H. bongeen has 4 pairs of calciferous glands and 2 pairs of (bidiverticulate) spermathecae. It is perhaps closest to *H. canaliculatus* (Fletcher, 1889) recorded from the Lachlan River at Forbes, NSW. It differs from *H. canaliculatus* in several

features but especially in lacking dorsal canaliculation, in having one fewer pairs of spermathecae and in the numbers and position of the genital markings. On these variations, together with its geographic location, it is separated from other species and it is named after its type location.

ECOLOGICAL/AGRONOMIC OBSERVATIONS

In the same samples, a native *Diporochaeta* sp. was also identified. Neither of these, nor any other worms, were found nearby, including under an adjacent sorghum (*Sorghum bicolor*) crop, despite an hour of searching. Perhaps cultivation, which has severe effects on burrow systems and soil physical properties, and aerial spraying of insecticides, are adverse to its survival. The worms were collected from opposite the local school and thereby in an area presumably less affected by application of biocides. A local farmer from Jondaryan (K. McIntyre, pers. comm.) reported that when the natural grasslands were first cultivated, masses of earthworms were exposed. Possibly the present population is residual from what must have been a very abundant fauna. The type locality was known to local fishermen in the 1950's as a good source of bait (C.H. Thompson, pers. comm.).

The behaviour of these long worms was to escape rapidly along their burrows but when caught they were only moderately active, although they exuded copious watery fluid which dripped from their bodies. The specimens were dug from burrows up to 1cm wide to a depth greater than 30cm. Waco clay is a strongly structured soil that has a thin, fine granular 'self-mulching' surface, but it is possible that the surface casting noted for this worm contributed to the granular aggregates observed. It is likely that their burrows extend down to the deep calcareous brown clay subsoils found at depths of up to 1m as during dry periods these deep subsoils would provide a moist retreat for earthworms.

The agronomic potential of collected specimens was investigated in a glasshouse experiment, probably the first assessment of this type for this genus. From twelve specimens, maintained in a sealed container filled with the soil for six months, four mature specimens (which had regressed to a "sub-adult" stage with suppressed clitella) were released into new soil in irrigated 18kg cores of clay. None survived after four months (October 1992-February 1993) when soil temperature ranged 17-35°C. Despite this, their burrows and granular casts indicated some

initial activity and the final yield of grain sorghum (*Sorghum bicolor*) was increased, compared to uninoculated controls, by 40%.

Heteropodrilus dioecius

(Stephenson, 1933)

(Fig. 2)

MATERIAL EXAMINED

2 mature specimens, QMG210139, Brookfield, Qld. (27°30'S, 152°55'E), C.H. Thompson, 17 May 92; CSIRO Samford farm, Qld. (27°22'S, 152°53'E), 5 mature specimens, R.J. Blakemore, 9 Apr 92 and 22 Jun 92, in author's collection.

HABITAT

Under litter on bank of river; on surface after rains.

EXTERNAL CHARACTERS

Length 58-70mm. Width 2.5-3mm. Segments 90-103, body cylindrical but segments tending to become trapezoid with only slight secondary annulation. Colour of anterior dorsum pigment light to dark brown, clitellum yellow-orange with faint iridescence, ventrum pale. Prostomium closed epilobous tapering to notch that extends dorsally to 1/2 (not as far in all specimens). First dorsal pore: 5/6 faint becoming obvious by 8/9 and either obvious and continuous over clitellum or not. Setae 8 per segment from ii; lateral setal couples widely spaced; setae *a* of vi to xii seen to be damaged or dehiscent in some specimens and, on xviii *a* setae may be modified. (Samford, 1.5:1:1.5:2.2:3.3:0.30); (Brookfield, 2:1:2:2:5:0.3). Nephropores in D line 1/2-3/4, 9/10 and 11/12 then alternating, C line in 4/5-8/9, in B line 10/11, 12/13 then alternating. There is clear alternation between B and D lines for most of body length (in one Brookfield specimen the alternation was asymmetrical within segments). Clitellum raised and cingular 1/3xiii, xiv-xvi, 1/3xvii (may be interrupted ventrally in xvii); furrows, setae and nephropores retained. Male pores not found. Female pores paired in xiv in common darker field antero-medial to *a* setae (more closely paired in Brookfield specimens). Spermathecal pores 6/7, 7/8 and 8/9 small and concealed in furrows in B line. Genital markings none, but in two Samford specimens, tumid pads seen in *aa* in x and/or xi and possibly small unpaired genital markings on xviii.

INTERNAL CHARACTERS

Septa 4/5-9/10 moderately thick, 8/9/10 the thickest, 10/11-14/15 weaker. Dorsal blood ves-

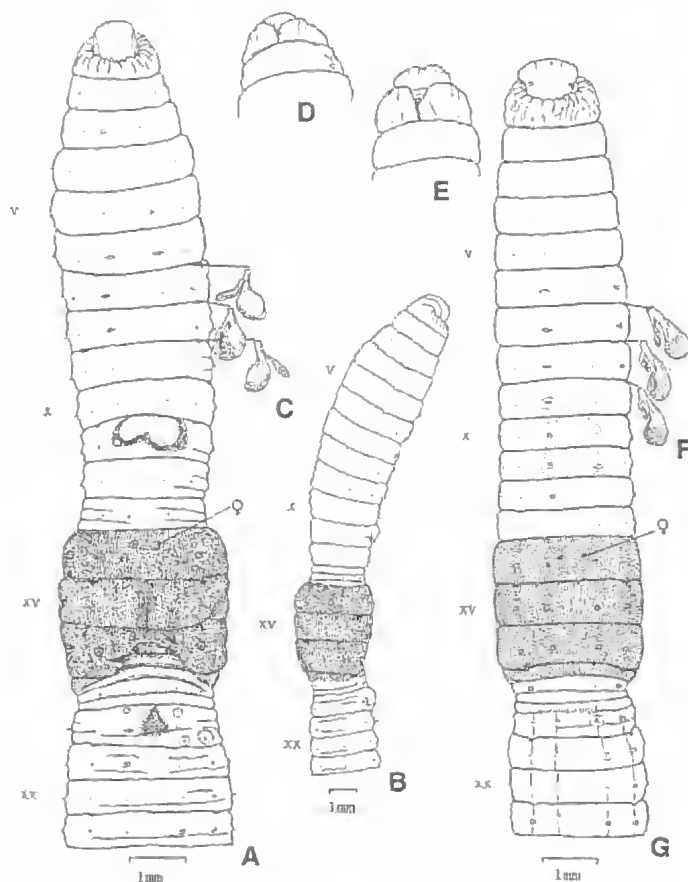


FIG. 2. *Heteroporodrilus dioecius*, Samford. A, ventral view; B, reduced lateral view; C, spermathecae; D, prostomium; E, prostomium of second specimen; G, ventral view; F, spermathecae. Prostates were aborted in all specimens.

sel single continues on pharynx. Hearts in x to xiii, commissurals in vi or vii-ix. Gizzard small and spherical, moderately muscular in v. Cal-ciferous glands 3 pairs, ventral on oesophagus in xi, xii and xiii. Intestine widening in xv, no typh-losole. Holonephridia with large bladders, seen from at least vi, alternating in position as for nephropores. Iridescent funnels of testes free, or in sacs, in x and xi, seminal vesicles in ix and xi/xii. Paired tufts of egg strings seen in xiii or in xii (this anomalous positioning was seen in two specimens from Samford). Prostates absent. Three pairs of spermathecae in vii-ix, spherical ampullae taper to ducts each with a medium length diverticulum (iridescent in several cases).

ciferous glands which are sessile rather than on short-stalks.

Heteroporodrilus doubei sp. nov. (Fig. 3)

MATERIAL EXAMINED

HOLOTYPE: QMG211897, 10km NW of Lismore, NSW, 28°48'S, 153°17'E, Dr. B. Doube, 26 Feb 1992, mature, drawn and dissected.

PARATYPES: QMG211898, mature complete; QMG211899, mature posterior amputee. Same collec-tion data as holotype.

Gut contents fine colloidal material, dead roots and organic debris.

REMARKS

This species was erected on aprostatic specimens from Toowoomba (Stephenson, 1933), but Jamieson (1970) collected specimens at Petrie near Brisbane that had racemose prostates and male pores. Possibly similarly male-fertile specimens were present in the populations from which aprostatic specimens were collected in the current study, as the diverticula were in-seminated.

These specimens from Sam-ford and Brookfield clearly lie within the descriptions of *H. dioecius*; a variation from Jamieson (1970) (apart from lack of prostates) is that the pros-tomium is here interpreted as being furrowed, closed epilobous rather than tanylobous. Seminal vesicles were recorded in several of these specimens in ix and xi/xii which is unusual and possibly the material filling xi was mucal coagulum. It is unusual too to observe ovaries in xii (i.e. progynous). Stephenson (1933) found in one specimen that one spermatheca, from the three pairs, was absent. Prostatic morphs of this species differ from *H. raveni* principally in having one fewer pairs of cal-

HABITAT

In deep unstructured black clay soil-prairie podsol in deep vertical burrows in association with a *Digaster* sp. nov.

EXTERNAL CHARACTERS

Length 95-120mm. Width 3.5-4.0mm. Segments 91 (holotype) body circular. Unpigmented, transparent in alcohol. Prostomium closed epilobous. First dorsal pore 5/6, not clear on clitellum. Setae 8 per segment from ii, *ab* absent from xviii, whole length of setae can be seen through body wall after clitellum (2.13:1.0:1.63:1.75:6.0:0.36). Nephropores in D in 1/2-3/4? and 6/7 on left hand side, in C 5/6-8/9 in B in 9/10 on right hand side and 10/11 on left hand side then alternating between D and B for remainder of body. Clitellum 1/2xiii-xvii pale coloured but slightly tumid. Male pores small in site of missing *b* setae on slightly raised mound. Female pore on xiv on left hand side only (holotype) or small and paired (paratype 1). Spermathecal pores concealed in furrows 7/8/9 in B. Genital markings single, ventrally offset disc on vii; two closely paired in anterior of viii with more lateral sets in longitudinal series in line with spermathecal pores; similar discs to viii on ix except the median discs are in the setal arc; possibly the raised mounds on xviii are genital markings. Markings not as distinct in paratypes.

INTERNAL CHARACTERS

Septa 5/6 weak and finely attached to sides and base of gizzard; 6/7-10/11 moderately thickened; 11/12 on thin. Dorsal blood vessel single onto pharyngeal mass in iv. Commissurals in vi-ix; hearts in x-xiii, the last three pairs larger. Ventral vessel bifurcated under gizzard. Fine, supra-oesophageal vessel seen in xii and xiii with lateral branches. Gizzard large, muscular in v but displaced almost to 6/7. Calciferous glands small, white, ventrally sessile pairs of glands in xi-xiii. Intestine widening suddenly in xv (acaecate, atyphlosolate). Holonephridia from anterior with large, flimsy vesicles obvious in the clitellar region, alternating in position. Testis/sperm funnels iridescent, seen in x and xi but fragmented during dissection; large pairs of racemose seminal vesicles posteriorly in ix and anteriorly in xii. Ovaries not located. Prostates tubulo-racemose, confined to xviii but folded over flaccid duct. Spermathecae two pairs in viii and ix, bulbous ampullae narrow to shorter ducts, each bearing a pair of opposed clavate, iridescent diverticula. Gut contents fine soil and *Acarina* (litter mites)

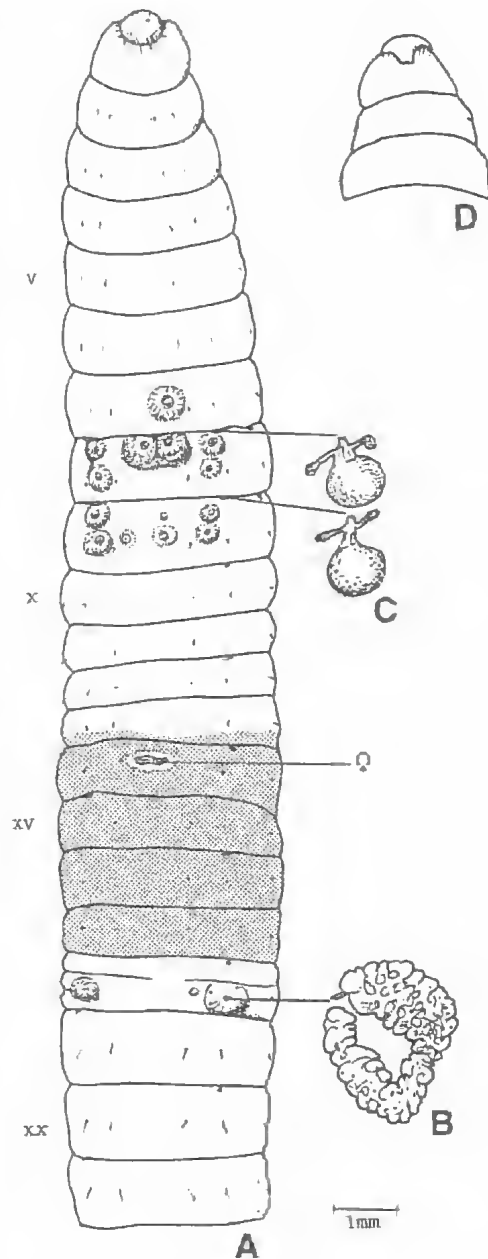


FIG. 3. *Heteroporodrilus doubei* sp. nov. A, ventral view; B, tubuloracemose prostate; C, spermathecae; D, prostomium.

suggesting geophagous/detritivores diet. Mucus invests several anterior segments.

REMARKS

Heteroporodrilus doubei has 3 pairs of calciferous glands and two pairs of bidiverticulate spermathecae, and is named after the collector. Similarities in allocation of calciferous glands and spermathecae are with *Heteroporodrilus minyoni* which, however, is much larger (400mm), and also with the bi-diverticulate *H. lamingtonensis* in which the position of the genital markings are in x and xi and xvi-xxi rather than in vii-ix.

Heteroporodrilus doubei vindicates the separation of *Heteroporodrilus* s. mihi from *Plutellus* s. stricto, outlined in the emendation of the genus above, as it has sessile calciferous glands and tubuloracemose prostates that would have bridged the previous generic definitions.

***Heteroporodrilus jamiesoni* sp. nov.**
(Fig. 4)

MATERIAL EXAMINED

HOLOTYPE: QMG211900, Mt Glorious, Qld, 27°20'S, 152°46'E, B. Jamieson collection, labelled "Or5 QSp 27", 12 Aug 1971, previously dissected mature specimen.

HABITAT

?rainforest

EXTERNAL CHARACTERS

Length 110mm (posterior amputee). Width 6mm. Segments 154+. Body spherical without dorsal canaliculation, peristomium wrinkled, preclitellar ventrum somewhat corrugated, secondary annulation slight. Unpigmented buff in alcohol, clitellum darker. Prostomium closed epilobous with distinct central cleft. First dorsal pore 6/7? wide, continuous on clitellum. Setae 8 per segment obvious from iii, *a* and *b* setae absent from xviii; lateral setal couples widely spaced (2.0:1.0:1.8:3.0:4.0:0.23). Nephropores at anterior margin of segments: ii/D, iii/D, iv/D or C, V/C, vi/C, vii/C, viii/C or D, ix/C or D, x/D, xi/B then symmetrically alternating for remainder of body. Clitellum annular $\frac{1}{2}$ xiii- $\frac{1}{2}$ xvii, interrupted ventrally in xvii. Furrows, setae and nephropores retained. Male pores on elongate porophores on xviii in B line. Female pores paired on xiv antero-median to *a* setae. Spermathecal pores five pairs 5/6-8/9 in B line. Genital markings in xvii-xx widely spaced by the width of the *a* setae, wholly presetal, laterally flattened pads which just impinge on the ventral setal couples.

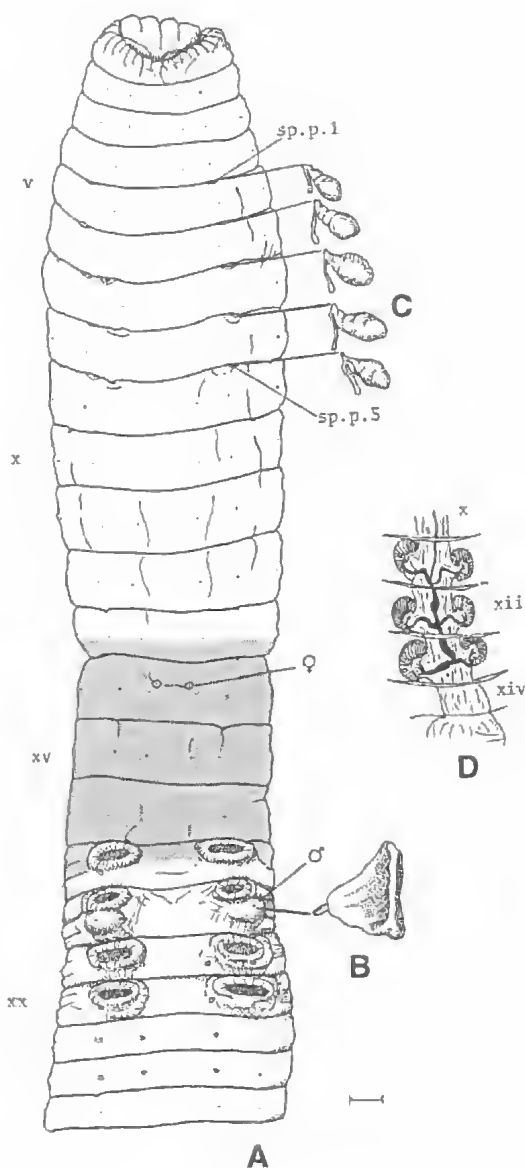


FIG. 4. *Heteroporodrilus jamiesoni* sp. nov. A, ventral view; B, prostate; C, spermathecae in situ; D, dorsal view of calciferous glands with the dorsal vessel removed. The peristomium was damaged dorsally and was not drawn.

INTERNAL CHARACTERS

Septa 5/6 weak, 6/7-12/13 becoming progressively stronger, then thinning; 5/6 and 6/7 displaced by gizzard, 10/11 and 11/12 converging and thickened. Dorsal blood vessel single con-

tinuous on pharynx. Commissurals noted in vi-ix, hearts in x-xiii. A supra-oesophageal vessel in x, strengthens from xi-xiii and, on each side, supplies the centre of each calciferous gland in these last three segments with a connective that dissipates into capillaries. (Ventral vessels not inspected). Gizzard muscular in v displacing septum 5/6 and 6/7, with wide rim anteriorly then tapering to appear cone shaped. On the oesophagus or posterior septum of vi-ix, small opalescent glands or sacs were also observed. Calciferous glands three pairs of spherical, almost reniform calciferous glands ventro-lateral to oesophagus in xi, xii, and xiii with numerous lamellae seen externally. To each gland a short stalk extends laterally from the oesophagus, and is directed downwards to the dorsal centre of each gland i.e. on short-stalks. Intestine widens in xv to reach its full width in xvi; typhlosole not found. Holonephric throughout with large convoluted tubes and flattened, round terminal bladders in the position of nephropores. Male organs holandric; especially x, but in xi too, fairly thickened pericardic (testis) sacs extend between the septa and encompass the blood vessels, oesophagus and the large iridescent funnels of the testes. Seminal vesicles are paired and racemose in ix posteriorly and xii anteriorly on septa. Ovaries small compact glands found in the anterior ventrum of xiii but individual ova not visible. Prostates compact, tongue-like, racemose glands confined to xviii each with a short, flaccid duct. Spermathecae five pairs in v-ix (the anterior pair obscured by gizzard and septa). Elongate, conical ampullae attach to tapering ducts each with a single simple digitiform diverticulum. The right side posterior diverticulum was bifid with a smaller, blunt branch. Iridescence was noted for each diverticulum. Gut contents almost entirely consisting of woody organic matter well mixed with some soil.

REMARKS

Heteropodrilus jamiesoni has three pairs of calciferous glands and five (or four) pairs of spermathecae and corresponds with Jamieson's (1970) Mt Glorious specimen he placed, despite several differences in the accounts, in *H. ashworthi* (Stephenson, 1933) (here considered a junior synonym of *H. oxleyensis*). The present specimen is especially similar with regards to the illustrations (Jamieson, 1970: figs 2; 3a; 8a,b; 9a; 10a). Differences are that only four, rather than five spermathecae were found, testis were free rather than in testis sacs as here and the ovaries and

funnels were (erroneously) recorded in xiv. Distributions of genital markings concur except for the absence in the specimen before me, of an obvious pair of presetal elliptical pads in ix and x.

This species can be separated from *H. oxleyensis* on the basis of genital markings, but not on testis sacs, which have been recorded as present or absent for both species. The spermathecae of *H. oxleyensis* and *H. jamiesoni* are similar in appearance and are recorded as 4 or 3 pairs and 5 or 4 pairs, respectively. Separating species principally on genital markings, which may vary with season or physiological or ontological state, is perhaps tenuous. But, in cases where population ranges overlap, such features are perhaps emphasised and may have a greater importance for speciation. Such small apparent variations in genital markings could be crucial deciders for mate recognition.

Of interest is that the short stalks on the calciferous glands in this specimen are similar to those for *H. oxleyensis* (Mt Cotton specimen) as well as those illustrated for *Heteropodrilus minyoni* comb. nov. (Dyde, 1980: fig. 2b).

Heteropodrilus oxleyensis

(Fletcher, 1889)

(Figs 5, 6)

MATERIAL EXAMINED

QMG210140, 2 mature, dissected specimens, Lower Savages Rd., Brookfield (27°30'S, 152°55'E), early mornings, C.H. Thompson, 17 May 1992; 1 mature specimen, same locality data as previous, 31 Dec 1992, author's collection; QMG210141, 1 mature specimen (with the posterior amputated but retained) and three sub-adult and two immature specimens, Queensland University farm, Mt Cotton (27°53'S, 153°14'E), R.J. Blakemore, S. Jeffries, 19 Jan 1993; sub-adult specimens, same collection data as previous, A. Wilkie, Aug & Oct, 1992, author's collection; one mature specimen, possibly a posterior amputee, Samford CSIRO farm (27°22'S, 152°53'E), R.J. Blakemore, V.R. Catchpoole, 5 Feb 1992, author's collection. Descriptions following are in the same order as the three locations.

HABITAT

On road near remnant rainforest; under 'blue gum' (*Eucalyptus tereticornis*) and *Leucaena leucocipha* plantation, particularly in red pod-solic soil; under grass in a non-calcic brown soil.

EXTERNAL CHARACTERS

Length of mature specimens: 100-120mm; 140mm; >92mm (less mature specimens: 33-110mm). Width of larger specimens: 5.5-6mm; 4mm; 5mm. Segments of mature specimens:

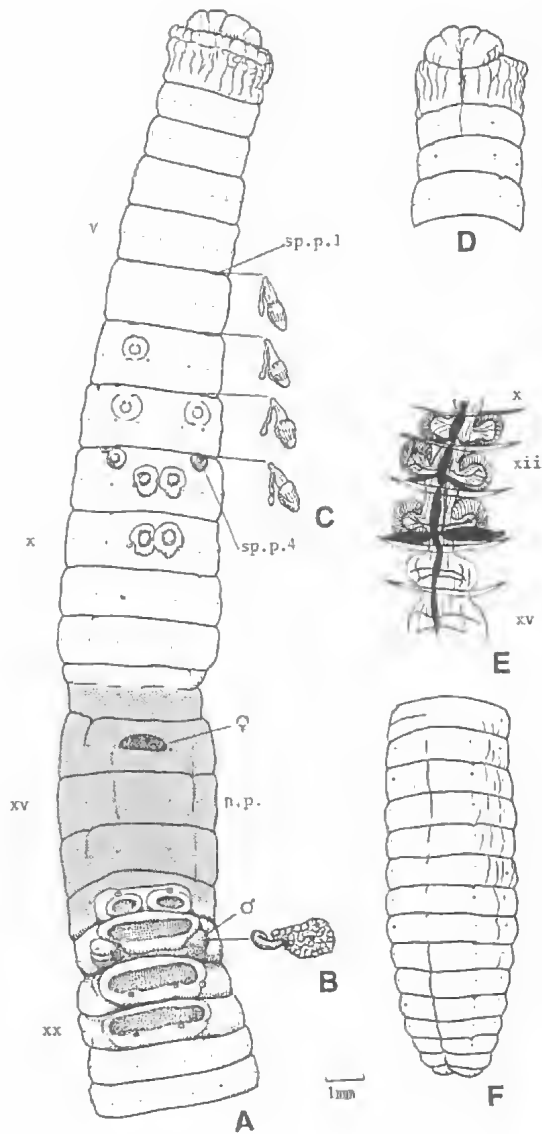


FIG. 5. *Heteroporodrilus oxleyensis*, Mt Cotton, mature specimen. A, ventral view; B, prostate; C, spermathecae in situ. D-F, dorsal views. D, prostomium; E, calciferous glands; F, posterior.

161, 185, 190; 167; >119 (others: 113-159). Secondary annulation minimal. Slight dorsal furrows in caudal segments. Colour of dorsum, especially in anterior and caudal segments, pigmented light yellowish-brown with slight iridescence (Samford specimen dark grey), ventrum pale; clitellum buff. Prostomium closed epilobous with

distinct dorsal cleft extending from tip of prostomium through to 1/2 or 2/3 (seen in all larger specimens). Immature specimens have furrow to 1/2 only but short grooves also flare from prostomial junction. Pharynx may evert on preservation. Peristomium usually rugose. First dorsal pore 5/6 faint, 6/7 wide; 6/7 rudimentary, from 7/8 distinct; obvious from 7/8. Setae 8 per segment from ii, *a* and *b* (always?) absent from xviii; lateral setal couples widely spaced, (2:1:2:2:4:3:0.27); (2.0:1.0:2.0:2.3:3.7:0.23); (2:1:2:2:3:0.3). Nephropores in D line 1/2-3/4, 5/6 or 6/7, then alternating; in C line, when not in D in 4/5-7/8 and alternating in B line from 9/10. Clear alternation between B and D lines for remainder of body. In some specimens,

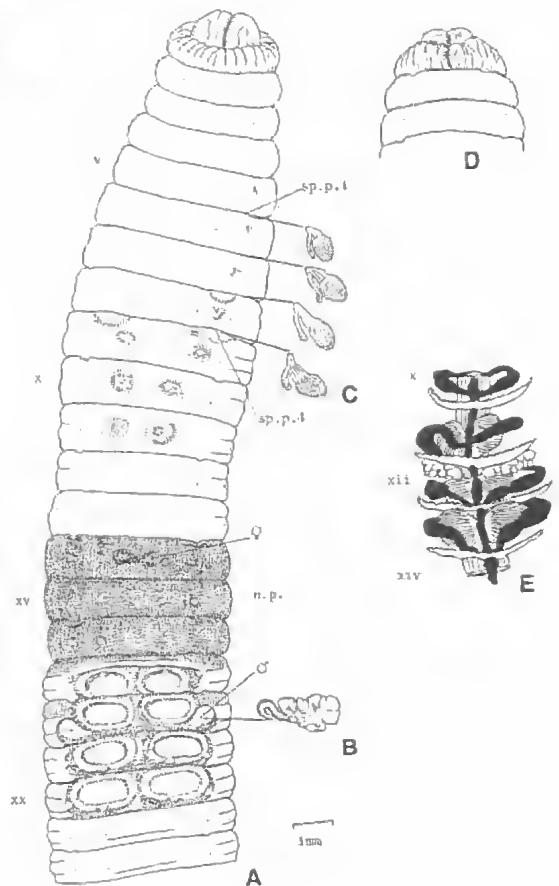


FIG. 6. *Heteroporodrilus oxleyensis*, Samford specimen. A, ventral view; B, prostate; C, spermathecae; D, prostomium; E, ventral view of calciferous glands.

nephropore alternations were asymmetrical in B and D per side. Clitellum $\frac{1}{2}$ xiii- $\frac{2}{3}$ xvii, xvii interrupted ventrally in xvii; setae, nephropores, furrows and dorsal pores retained. Male pores on xviii on slightly raised porophores, approximately in B line (on immature and subadult specimens seen within small lateral creases). Female pores on xiv a pair anterior-medial to a setae in common darker lateral patch. Spermathecal pores four pairs in 5/6-8/9 in furrows in B line. Genital markings of Brookfield specimens: in some of vi-xi small closely paired, median pads, in xvii closely paired or elongate postsetal pads, xviii-xx (and xxi in one unusual specimen) tumid, elongate, mostly presetal pads; Mt Cotton: in vii and viii single or paired faint discs anterior to ventral setal couples, in ix and x closely paired discs between a setae, also in ix a smaller pair of markings just behind the spermathecal pores, in xvii a pair of postsetal pads, closely paired in common ventral tumid area and mostly presetal in each of xviii-xx; elongate smooth pads sunken in otherwise raised glandular areas; Samford: in ix-xi small, ventrally paired discs, in xvii postsetally and presetal in xviii-xx large, paired pads elongate from mid-ventrum to B lines.

INTERNAL CHARACTERS

Septa 4/5 membranous to anterior of gizzard, 5/6 thin and much displaced to accommodate gizzard, 6/7-11/12 only slight, but progressive thickening, 12/13-14/15 thinning and thereafter membranous. Septa 4/5-8/9 are posteriorly displaced to a lessening degree, 9/10 and 10/11 are adherent. Pharyngeal tendons extend through anterior septa. Dorsal blood vessel single continuous onto pharynx. Commissurals from vi-x, hearts in xi-xiii. In Mt Cotton specimens: supraoesophageal vessel not found in xi but developed in xii and xiii with small connective to dorsal heart valves and lateral branches attached to stout pink stalks that pass to dorsal centres of the calciferous glands on each side. The hearts pass to ventral vessel, dorsal to which is a separate vessel that seems to supply the calciferous glands at their ventral axes. The dorsal vessel from xiv has two small pairs of vessels in each segment that pass to each side of the alimentary canal. Gizzard tubular to spherical and muscular in v. Calciferous glands three pairs in xi, xii, and xiii; spherical glands with white lamellae in section and visible externally, lay ventro-lateral to the oesophagus on short stalks (in one Brookfield specimen the glands are anomalous in xi then in

xiv and xv on left side only). Intestine widening through xv; no typhlosole. Nephridia paired holonephridia with long convoluted tubes and deflated, subspherical to elongate, terminal bladders, from at least v, corresponding in position to the nephropores. Iridescent testes and funnels ventrally in x and xi within pericardic testis sacs (strong in x, more membranous in xi); a small pair of racemose seminal vesicles posteriorly on septa in ix (and xi) and (lobulate) anteriorly in xii. A compact pair of glandular ovaries (individual ova not discernible) in anterior and nebulous oviducts in posterior of xiii. Prostates paired racemose glands, confined to xviii each with a short, ensheathed duct bent in single loop. Spermathecae four pairs in vi-ix; conical, fleckled ampullae connect to tapering ducts each with a single diverticulum. Iridescent (inseminated) diverticula only noted in Samford specimen. Gut contents mostly organic matter including woody (dead root) material, plus some fine and some coarser soil.

REMARKS

Despite some variation between the specimens described above from the three locations, it was decided to include this new material in *H. oxleyensis*. The original brief description by Fletcher (1889) was based on one acitellate specimen (plus two incomplete specimens). Subadult specimens from Mt Cotton differ insubstantially from this original description apart from having about 15-20 fewer segments. Moreover, the mature specimens from Mt Cotton and the other two locations above agree sufficiently with each other and with Stephenson's (1933) single specimen of *Woodwardiella ashworthi*, here regarded as a junior synonym of *H. oxleyensis*.

Justification for this synonymy is that Stephenson (1933) omitted to refer to the earlier description, yet his specimen from Brisbane agrees on every point in common with Fletcher's (1889) *H. oxleyensis* apart from those attributable to its being mature. The only other records of *H. oxleyensis* are the two specimens (from Kholo Creek and Marrickville) described and illustrated by Jamieson (1970). These also concur with Stephenson's (1933) specimen except that they are slightly truncated, have dorsal pores in 5/6 or 6/7 (rather than 7/8), do not retain setae a of xviii, one has three pairs of spermathecae (rather than four) and they have paired postsetal genital markings in xvii (rather than an analogue, Stephenson, 1933: fig. 12).

***Heteroporodrilus
thompsoni* sp. nov.**
(Fig. 7)

MATERIAL EXAMINED

HOLOTYPE: QMG210142, Lower Savages Rd. and near Gold Creek, Brookfield, Qld (27°30'S, 152°55'E), C. H. Thompson, 08 Apr 1992.

PARATYPES: 6 specimens, QMG210143- G210146, same collection data as holotype, 15 Apr 1992, 17 May 1992, 30 Dec 1992.

HABITAT

Under leaf litter of rain-forest and eucalypt woodland and on road surface, especially after rain.

EXTERNAL CHARACTERS

Length 210-270mm (holotype: 210mm, but some damage to middle area). Mass 21.5g (holotype). Width (midclitellar) 11-13mm. Segments 181-235, (holotype 235). Faint secondary annulation, especially after the clitellum. One specimen had marked dorsal furrow (i.e. canaliculate) in the latter half of its body. Unpigmented, grey in alcohol; clitellum darker pink-grey and faintly iridescent. Prostomium closed epilobous to pro-epilobous with definite furrow that bisects prostomium and extends to 2/3 as a groove. Peristomium rugose. First dorsal pore not clearly detectable in deep furrows but seen in 10/11 and 13/14 at least, and again from 17/18. Setae 8 per segment, from ii, dark tipped, *ab* absent from xviii (mean of four specimens; 1.7:1.0:1.5:2.5:3.8:0.26). Nephropores at anterior margin of segment almost in furrow, obvious on clitellum. The most common arrangements: ii/D, iii/D, iv/C or D, V/C, vi/C, vii/C, viii/C or D, ix/D or C, x/B, xi/D, xii/B, xiii/D, xiv/B, xv/D, xvi/B, xviii/D, xviii/B, xix/D, xx/B, xxi/D, etc. Several specimens had irregular pore distributions to the above scheme, one had the opposite arrangement from x,

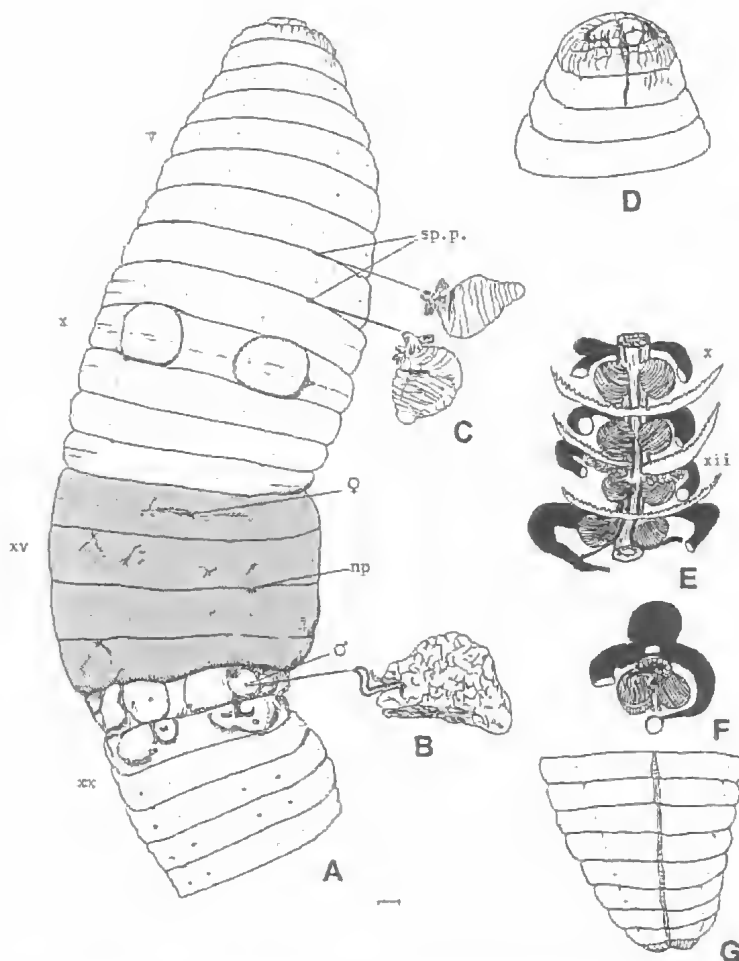


FIG. 7. *Heteroporodrilus thompsoni*. A, ventral view of paratype; B, prostate; C, spermathecae in situ; D, dorsal view of prostomium; E, ventral view of calciferous glands with ventral vessel cut away; F, anterior view of calciferous glands from xiii with left-side sectioned; G, posterior.

Confusion over the definition of *H. oxleyensis* that resulted mainly from its designation on sub-adult material (as was *H. sloanei*, also by Fletcher, 1889) has been reduced by this revision. The combination of three pairs of calciferous glands in xi-xiii (mislabelled in Jamieson, 1970: figs. 3d, 5g as in ix), four (or three) pairs of spermathecae and postsetal genital markings in xvii are unique to this species. The distribution in the Brisbane region of southeast Qld. is dissipated only by the one anomalous record from the suburb of Marrickville, Sydney, NSW (collector M.E. Grey, 1933).

another two had asymmetrical alternations within a segment (i.e. a pore in B and one in D). Clitellum annular and tumid xiv-xvii, setae and nephropores retained often in deep dimples. Male pores in xviii in site of *b* setae on slightly raised porophore. Female pores on xiv variously closely paired antero-medial to *aa*, sometimes concealed in a lateral groove, alternatively a single pore on a slightly tumid pad antero-medial to *aa* setae. Spermathecal pores two pairs in 7/8 and 8/9 almost hidden in furrows in B line but visible under traction. Genital markings in x in all specimens: a distinct pair of circular, tumid pads occupying the longitudinal width of the segment and encompassing the ventral setal pairs. In xviii, the areas of the missing ventral setal couples are generally tumid with a mid-ventral hollow and in xix is a similar glandular area which extends as far as the limit of the ventral setae.

INTERNAL CHARACTERS

Septa 4/5-7/8 moderately thickened, 8/9-12/13 becoming progressively much thicker, then, after 13/14, thinning. Dorsal blood vessel single, continuous on pharynx. Commissurals in vii-ix, large hearts in x-xiii. From ix or x to xiv or xv large bladders dominate the dorsal vessels, in xv the enlarged dorsal vessel has two pairs of ventrally directed vessels which surround the oesophageal valve. Bifurcate ventral blood vessels form a pair of hairpin loops under gizzard before moving anteriorly. Gizzard large, muscular and barrel shaped in v with slight anterior rim, compressing septa 5/6 onto 6/7 and reaching as far back as vii. Calciferous glands four pairs in x-xiii, the anterior pair the smallest, as spherical, white, ventral pouches sessile on oesophagus each with numerous fine lamellae internally. A pair of sub-oesophageal blood vessels run between the lobes of each pair of glands. Intestine origin abrupt in xv or xvi, no typhlosole. Holonephric, with large, subspherical to elongate, flattened bladders corresponding in position with external nephropores. Male organs holandric: large paired, iridescent funnels of testes free (or appearing in testis sacs in at least two specimens) in x and xi. Seminal vesicles medium to small size, paired and racemose in ix and xii (the latter lobulated on anterior septum). In ix white coagulum, the same texture as in seminal vesicles, frequently seen. Ovaries as a small pair of egg-string tufts anteriorly in xiii and paired diaphanous oviducts on posterior ventrum. Prostates con-

fined to xviii, a pair of compact, squarish, racemose glands with short, bent duct joined entally by vasa deferentia. In section the prostates appear solid without obvious central lumina. Spermathecae two pairs in viii and ix: large bulbous but slightly deflated or deflected subspherical ampullae with fine concertina-like corrugations, attach to shortish ducts bearing several (two to six), small digitiform or bi-, tri-, or multi-lobed diverticula encircling the duct near the ectal end. Stalks (and occasionally termina) of several diverticula have lustre indicating insemination. Gut contents mostly reddish silt with some grits and sometimes organic debris including woody remains (geophagous/detritivorous).

REMARKS

The combinations of four pairs of calciferous glands and two pairs of polydiverticulate spermathecae identify *H. thompsoni* which is named after the collector. This species has close affinities with the similarly large *H. tryoni*, also collected from this location. It differs from *H. tryoni* in having one fewer pair of calciferous glands, one fewer pair of spermathecae, different setal ratios and in having a distinct pair of genital markings in x. *H. tryoni* usually has a pair or trio of tortuous diverticula on each of its three pairs of spermathecae, often with sessile seminal chambers. It is noteworthy that Boardman's (1932) description for *H. youngi* (syn. *H. tryoni*) has compound diverticula similar to those described here for *H. thompsoni*, but here again there are three pairs of spermathecae (even in his paratype where he reports only dissecting the first two spermathecae from segment vii and viii).

Heteropodrilus tryoni (Fletcher, 1889) (Fig. 8)

MATERIAL EXAMINED

QMG210147, Adayale St and Lower Savages Rd, Brookfield, Qld. (27°30'S, 152°55'E), C.H. Thompson, 8 Apr 1992, one damaged mature specimen dissected and drawn; QMG210148, 17 May 1992, one intact specimen; QMG210149, 26 May 1992, two damaged specimens dissected.

HABITAT

Under litter, on surface after rains and at about 30 cm depth in a deep surfaced eucrozem soil with clay-loam surface texture (field pH 6.0).

EXTERNAL CHARACTERS

Length 270-300mm. Mass 35.85g (damaged but complete specimen). Width (midclitellar) 14-17mm. Segments: 235-236. Peristomium wrinkled, second segment less so. Marked dorsal furrow in latter part of body. Pigmented dorsum dark grey in alcohol; clitellum slightly darker with faint green tinge. Prostomium closed epilobous to pro-epilobous with definite furrow that bisects prostomium and extends to 2/3 as a groove. First dorsal pore in 6/7 or 7/8. Setae small, 8 per segment from ii, ventral setal couples widely spaced; ventral setae absent on xviii. (mean; 2.0:1.0:1.8:3.5:4.3:0.24). Nephropores at anterior margin of segment in furrow, irregular alterations noted for two specimens: ii/DD, iii/DD, iv/DD, v/CC, vi/DB, vii/CD, viii/DC, ix/CD, x/DC, xi/CD, xii/DB, xiii/BD, xiv/DB, xv/BD, xvi/DB, xvii/BD, xviii/DB, xix/BD, xx/DB, xxi/BD this alternation continued for the remainder of the bodies Nephropores do not open in B lines in vii, viii nor ix as these positions are occupied by the spermathecal pores. Clitellum annular and tumid; 1/2xiii, xiv-xvii but interrupted ventrally on xvii by genital markings. Setae and nephropores retained. Male pores paired in xviii on small circular porophores at centre of generally tumid patch centred at site of aborted *b* setae. Female pores on xiv in lateral groove stretching between *a* setae, but just anterior to setal arc. Spermathecal pores in 6/7, 7/8 and 8/9 almost hidden in furrows in B line but visible under traction as minute pores. Accessory genital markings in x and xi slightly raised pair of tumid pads filling the anterior aspects and just incorporating the ventral setal pairs; in xvii a pair of sucker-like markings with the ventral setae in the lower edge; in xix a similar pair of pads although possibly slightly wider.

INTERNAL CHARACTERS

Septa 5/6 and 6/7 weak but adpressed, 7/8-12/13 thick, 13/14 moderately thick, thereafter membranous. Dorsal blood vessel: single and considerable. Commissurals in vii-ix, large hearts in x-xiii. Gizzard moderately muscular and cone shaped in v with wider anterior rim. Calciferous glands five pairs in ix-xiii, the anterior pair the smallest, as spherical, white, ventral pouches sessile on oesophagus each with numerous fine lamellae internally. Intestine origin in xv, no typhlosole. Holonephridia with largish, subspherical collapsed bladders in position of external

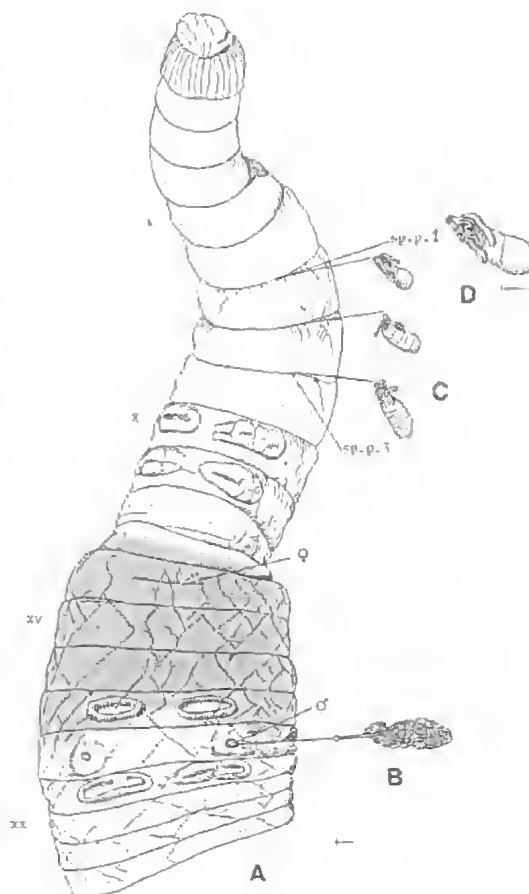


FIG. 8. *Heteroporodrilus tryoni*. A, ventral view of an anteriorly damaged specimen; B, prostate gland; C, spermathecae in situ; D, enlargement of a spermathecae.

nephropores. Iridescent funnels of testes free in x and xi close to ventral nerve cord. Seminal vesicles small and racemose in ix and xii. Ovaries as tufted strings in xiii with paired egg funnels on posterior ventrum. Prostates confined to xviii, a pair of tongue-like racemose glands with thin, straight, non-muscular duct. Spermathecae three pairs in vii, viii and ix: constricted, bulbous ampullae narrow abruptly to ducts bearing ventrally, three medium-sized, tortuous diverticula. The central diverticulum in each case was the most convoluted. Iridescence was seen in all diverticula. The same grey coagulum as was found in the body cavity reappeared in the gut. The ingesta was mainly dead plant remains including large woody husks and small leaf skeletons.

Port Macquarie, NSW (31°27'S, 152°55'E), B.G.M. Jamieson collection: 2 specimens (mixed with species of several other native genera): one acitellate, one posterior amputee at 16/17; both drawn and described here, 8 miles from Beechwood on Bellangry and Wilson River St. Forest Rd. Riverine forest sloping into gully, black soil under logs and in earth, W. Nash, R. Raven, 17 Jul 1975; 5 specimens tagged PH1 - PH5 (PH1 dissected, PH2 drawn, other specimens inspected), near Cairncross State Forest, 6.4km S of Telegraph Point turnoff by Pacific Hwy. Wet black soil in paperbark and tea trec swamp, W. Nash, R. Raven, 16 Jul 1975.

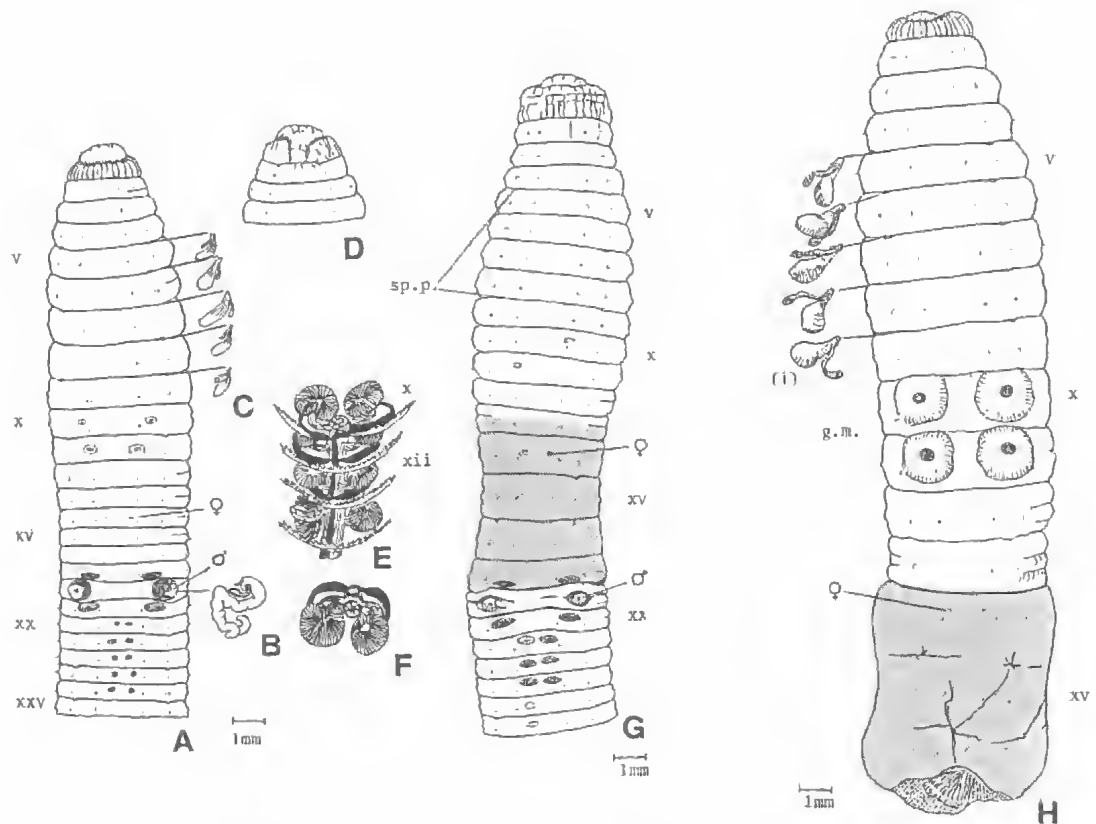


FIG. 9. *Plutellus heteroporus*. A, ventral view of acitellate specimen; B, tubular prostate; C, spermathecae; D, prostomium; E, dorsal view of calciferous glands in situ; F, anterior view of calciferous glands of xiii showing long ducts beneath lateral hearts; G, ventral view of specimen PH2; H, ventral view of posterior amputee specimen; I, spermathecae in situ (prostates lost).

EXTERNAL CHARACTERS

Length 77-175mm. Width 4-5mm. Segments 185-209. Body circular in section with secondary annulation dorsal from x and in post-clitellar segments. Pigmentless buff in alcohol, not iridescent, clitella manilla. Setal lines appear darker in some specimens. Prostomium tanylobous. First dorsal pore 7/8. Setae, especially ventral couples, dark, 8 per segment from ii, *a* and *b* absent from xviii, (mean of three setal ratios, 1.7:1.0:2.3:2.1:2.9:0.2). Nephropores paired in D line 1/2, 7/8, 9/10, 11/12, 13/14, 15/16, 17/18, etc.; in C line 2/3, 3/4, 4/5, 5/6 (one specimen in 6/7 too, another specimen in 8/9 also); in B line 6/7?, 8/9, 10/11, 12/13, 14/15, 16/17, 18/19, etc. One specimen had irregular alternations, but mostly alternation between D and B in successive segments. Clitellum $\frac{1}{3}$ xiii(dorsally), xiv-xvii annular, setae and nephropores retained, intersegmental furrows faint, dorsal pores occluded. Male

pores minute in xviii on small raised porophores in B line, each within a smooth, flattened, subspherical dish that fills the segment longitudinally. Female pores in xiv a minute pair widely spaced but antero-medial to *a* setae. Spermathecal pores five pairs in B lines from 4/5 - 8/9. Accessory genital markings in one specimen, a pair of large but lowset presetal pads with darker centres between *ab* in x and xi extending from the setal arc to the anterior furrow. In other specimens, these marks were not clearly defined but a similar pair of pads were present in ore in xi, on the left side only in one and in xii in another. Postsetally in xvii, a pair of ellipsoid smooth dishes between *ab* with translucent centres and shelving towards xviii; in xix a similar pair of marks presetally. Ellipsoid dishes, presetal, closely paired (occasionally single) and ventral to *aa* also present in each specimen in some of xx-xxiv (commonly in xx-xxii).

INTERNAL CHARACTERS

Septa 4/5 membranous, 5/6-12/13 moderately thickened (especially the first three impinging rearwards), 13/14 and 14/15 thinner, then membranous. Dorsal blood vessel single continues on pharynx. Commissurals vi-ix, larger hearts in x-xii. Gizzard thin walled but muscular in v, tubular or tapering. Calciferous glands four pairs laterally in x, xi, xii and xiii; rosette or reniform with radiating lamellae attaching to the oesophagus dorso-laterally via long curved ducts, one from each gland. Ducts well supplied with blood capillaries and originate near the centre of each gland. The glands are solid and consist of numerous internal lamellae. Oesophagus narrows in xiv (valve?) then widens in xv as intestine proper; in xv and xvi it is especially dilated; typhlosome and caeca not seen. Holonephric from ii. Large elongate bladders are associated with the nephropores i.e. they have alternate extensions in successive segments for most of the body. Iridescent funnels of testes free in x and xi; racemose seminal vesicles occupy ix and xii. Ovaries paired ventrally in xiii, numerous egg strings are loosely attached to give fan-like appearance. Prostates a pair of elongate and tortuous tubular prostates (internal lumina not visible) overlaying short muscular ducts (dilated near body wall) in xviii. The prostates extend from xviii to xix (one abnormal specimen had a continuation of the gland directed forwards as far as xvi). Spermathecae five pairs in v-ix; elongate ampullae taper to narrowing ducts each bearing a single clavate diverticulum on stalks almost as long as ampulla (in mature specimens the diverticular bulbs were iridescent). Gut contents colloidal dark soil with no obvious organic debris.

REMARKS

The above specimens correspond with previous descriptions of the type-series of the genus *Plutellus*, in particular that of Jamieson (1971a). Additional features recorded here are the first nepridiopores in D line in 1/2, new body dimensions, segmental counts, setal ratios and accessory genital markings. Large ventral disks in x and xi developed in one specimen resemble those seen in *P. manifestus* (see Jamieson, 1970: fig 6a). New illustrations are provided.

Plutellus heteroporus has very close affinities with *P. manifestus* from NSW and *P. hutchingsae* from Lord Howe Island, not least in having tubular prostates. Characteristics of the genus are the alternation of nephropores and, separating it from both the allied Australian genera

Heteropodrilus and the monotypic Lord Howe Island *Paraplutellus* Jamieson, 1972 (see Jamieson, 1977) the possession of four pairs of clearly stalked calciferous glands.

Jamieson (1971a), related how two lots of specimens were mixed in the same bottle in the Paris museum where Perrier first described type material in 1873. At about the same time, *Digaster lumbricoides* Perrier, 1872 was erected from specimens collected at Port Macquarie in 1846 (by M. Le Souef?). It is significant that this locality is the same as for the *P. heteroporus* specimens described above. The provenance of this new material then, supports the probable type-locality as being in Australia, and in particular Port Macquarie NSW, rather than Pennsylvania, (USA) as was presumed by Perrier.

DISCUSSION

Plutellus clearly retains the more 'primitive' tubular form of prostates, *Heteropodrilus* is thus considered an apomorphic sibling-group of *Plutellus* that has reached a climax in rainforest and riverine environments in the Qld. subtropics. This view contrasts with that of Dyne (1981: 105) who considered sessile calciferous glands as a plesiomorphic condition and the stalk-glanded *Plutellus* as the more derived genus.

Evidence that *Heteropodrilus* has diversified in south-east Qld. is provided here by surveys that have located four of the six previously described species for this region, and added several more to the list. One small area at Brookfield in Brisbane has yielded four species in association: *H. tryoni*, *H. thompsoni*, *H. dioecius*, *H. oxleyensis*, often in the same sample. If the origin of the genus is taken to be south-east Qld., then the focus of endemism (as indicated by the abundance and diversity of species and specimens) may well be in the catchments and rainforest foothills of the D'Aguilar Range of which Mt Glorious is a high point. Nevertheless, the diversity of *Heteropodrilus* species around Brisbane may be an aberration of sampling effort especially as much of the inland areas of the eastern sub-region have yet to be systematically sampled and are expected to provide further species. A fuller picture of the biogeography, as with the systematics of these and other species, may await genetic analyses.

That the types of *H. dioecius* were from Toowoomba on the Great Dividing Range demonstrate that this escarpment is no barrier to heteropodrilid migration. Another species,

H. bongeen, was recorded from the Condamine River plain west of Toowoomba in the Darling Downs region. This river, which at one time may have united with the Burnett River, eventually connects with the Murray-Darling river systems of New South Wales, Victoria and South Australia where distributions of other *Heteropodrilus* spp. have been recorded. The riverine transport mechanism for this genus is thus supported. The propensity for nocturnal or crepuscular wanderings (particularly after flooding?), noted for several species above, may further enhance their ability to disperse.

Several members of this genus are associated with riparian habitats where their burrows can easily access the water-table, they may thus survive apparently dry conditions. Osmotic regulation and secretion via large, exonephric terminal bladders, are perhaps enhanced by nephrophore alternation. Possibly this adaptation serves partly to maintain a more even body surface moisture, for respiration, lubrication and defence, especially in worms with larger surface areas, than would a regular series of nephropores. Both *Plutellus* and *Heteropodrilus* contain medium to large sized members. However, alternation of nephropores is found in other genera too eg. *Maoridrilus* Michaelsen, 1899, from New Zealand and in at least one member of the Australian native *Diploptrema* (*D. heteropora* Dyne, 1979).

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